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Opportunistic top predators partition food resources in a tropical freshwater ecosystem

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Abstract

- 1. The structure of food webs may be strongly influenced by the distribution of top predators in space and time. The Amazon biome is the only region in the world where four alligatorid species are known to occur in sympatry, and they attain high densities in some regions. As top predators with a diverse range of prey species occupying different trophic levels, their impact upon food webs should be substantial, but the degree to which crocodilians differ in their food sources, and potentially avoid competitive exclusion where they occur syntopically is not well understood.
- 2. Although most crocodilians are considered generalist opportunistic predators that feed on any source of protein available in the environment, Amazonian crocodilians show broad differences in the proportions of prey items they consume. It is believed that these differences may in part reflect habitat use, but it is unknown to what extent they represent interspecific differences in prey preferences or are a direct function of habitat selection.
- 3. Stable carbon isotope data (δ^{13} C) of crocodilians and their potential prey were used to assess differences in reliance on terrestrial versus aquatic resources. These data were then placed in a spatial context using classified maps that reflect habitat types (headwater streams, mid-order flooded-forest streams and *várzea* floodplains) to elucidate whether dietary differences are explained by habitat selection or are more likely a reflection of prey preferences.
- 4. We found evidence for differences in types of basal resources supporting these crocodilians. Mean δ^{13} C values were highest in *Paleosuchus trigonatus* (Schneider's dwarf caiman, $-25.7 \pm 1.2\%$), intermediate in *Caiman crocodilus* (spectacled caiman, $-27.4 \pm 1.2\%$) and *Paleosuchus palpebrosus* (Cuvier's dwarf caiman, $-27.7 \pm 1.1\%$) and lowest in *Melanosuchus niger* (black caiman, $-29.9 \pm 1.3\%$).
- 5. A progressive decrease in δ^{13} C values of crocodilian tissues occurred from headwaters to floodplains, which most likely reflects a progressive increase in autochthonous over allochthonous inputs in lower reaches of streams. The shift from terrestrial to aquatic resources sustaining these sympatric predators mirrors their spatial distribution along this ecotone. However, after taking into account the habitat in which pairs of syntopic individuals of distinct species occurred, significant differences in δ^{13} C values suggest that *P. trigonatus* and *P. palpebrosus* have

different prey bases. Thus, despite being opportunistic predators, our results show that differences in crocodilian diets likely result from prey preferences and not only from habitat selection. These findings suggest that some species of crocodilians may be less generalist than traditionally thought and their influence on terrestrial or aquatic food webs might be species specific.

KEYWORDS

aquatic food webs, crocodilians, spatial partitioning, terrestrial subsidies, trophic interactions

1 | INTRODUCTION

The diversity of coexisting species within ecological communities is partly determined by the ways in which they partition available resources (Finke & Snyder, 2008). Coexisting species must differ in their ecological requirements for a limiting shared resource by at least some minimal amount to avoid competitive exclusion (Pianka, 1974). One way in which different organisms directly interact with one another is through interspecific territorial interactions (Pulliam, 2000). This implies that stronger competitors might displace others from the most suitable areas. The Amazon biome is the only region known to sustain four alligatorid species living in sympatry. Given the high abundances of sympatric crocodilians (up to 450 individuals/km of shoreline) in some parts of the Amazon basin (Da Silveira, 2002), it is likely that resource partitioning contributes to their coexistence.

Most crocodilians are considered generalist opportunistic predators that take advantage of any available source of animal protein (Pooley, 1989). Amazonian crocodilians partition space, with each species occurring most frequently in specific habitats such as headwaters, flooded-forest streams or floodplain lakes (Magnusson, 1985); thus, it is expected that their diets will vary depending on the availability of different prey in each habitat type. However, the extent to which habitat selection influences food habits of Amazonian crocodilians is unknown (Magnusson, da Silva, & Lima, 1987). Furthermore, all four species occur in syntopy in some waterbodies in the Amazon basin (Marioni, Araujo, Villamarín, & Da Silveira, 2013). Within the same habitat type, prey partitioning might be a mechanism facilitating coexistence.

Crocodilians in general experience ontogenetic diet shifts starting from terrestrial and aquatic invertebrates when young, to more protein-rich diets in terms of biomass, composed mostly of fish and terrestrial vertebrates as they grow (Radloff, Hobson, & Leslie, 2012; Ross, 1998). Amazonian crocodilians (Alligatoridae) show this ontogenetic variation, but exhibit interspecific differences in diet as adults. Adult *Paleosuchus palpebrosus, Caiman crocodilus* and *Melanosuchus niger* attain up to 1.0, 1.4 and 2.5 m snout-vent length (SVL) respectively (Magnusson & Campos, 2010a; Thorbjarnarson, 2010; Velasco, Ayarzagüena, Manolis, & Stevenson, 2010). These species are common in open-canopy waterbodies and floodplains and have diets mostly composed of fish (Da Silveira & Magnusson, 1999; Magnusson et al., 1987). In contrast, adults of *Paleosuchus trigonatus*, which are most common in closed-canopy headwater streams and can attain over 1.0 m of SVL (Magnusson & Campos, 2010b), consume many terrestrial vertebrates, but few fish (Magnusson et al., 1987).

Historically, researchers have used "snap-shot" techniques such as stomach-content analysis to examine resource-use patterns of crocodilians (Magnusson et al., 1987; Webb, Manolis, & Buckworth, 1982). However, characterisation of time-integrated resource-use patterns requires repetitive observations from the same individual.

Over the past few decades, stable isotope analysis (SIA) has become an important tool, able to overcome sampling limitations because it is based on the principle that tissues of consumers reflect isotopic compositions of their diet in a predictable way (DeNiro & Epstein, 1978). Stable carbon isotope ratios (¹³C;¹²C; δ^{13} C) in aquatic plants depend on source isotopic values of inorganic C and aquatic CO₂, among other factors (Finlay, 2004; Finlay, Power, & Cabana, 1999; Keeley & Sandquist, 1992), and may be differentiated from terrestrial plant resources which vary substantially depending on photosynthetic pathways. Furthermore, δ^{13} C values change little with trophic transfers (DeNiro & Epstein, 1978; Peterson & Fry, 1987; Post, 2002). Thus, when source δ^{13} C values are different, isotopic composition of predators and their prey allows the use of mixing models to estimate the proportional contributions of different resources to consumer diets (Phillips et al., 2014).

In aquatic systems, the use of isotopic approaches has been integrated with spatial analyses to allow characterisation of dietary patterns by consumers in different habitat types (Jardine et al., 2012; Villamarín et al., 2016). In the Amazon basin, remote-sensing images have been increasingly used to answer ecological questions over large geographical scales (Melack et al., 2004; Villamarín et al., 2011). L-band synthetic aperture radar (SAR) imagery has been particularly useful due to the capacity to detect water under canopy cover. Thus, SAR has been used to estimate the extent of wetlands and generate accurate classification maps of vegetation types and flooding states throughout the Amazon basin (Hess, Melack, Novo, Barbosa, & Gastil, 2003, 2012; Hess et al., 2015; Rosenqvist, Forsberg, Pimentel, Rauste, & Richey, 2002). This allows quantification of available habitat types for crocodilians.

Here, we explore dietary patterns in four species of crocodilians across a wide area of central Amazonia, which encompasses an ecotone including the main habitat types where crocodilians occur. Findings from this study may contribute to refine our understanding

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about crocodilian diet and flux of energy in food webs by estimating the proportions of aquatic versus terrestrial resources that sustain these predators. Furthermore, our results may transform the way that people think about these opportunistic predators by providing evidence suggesting that species divergences in diet result from prey preferences and not only from habitat selection. Therefore, we used δ^{13} C values measured in crocodilian tissues and their prey, and placed them in a spatial context using maps that reflect habitat types to answer the following questions: (1) To what extent do Amazonian crocodilians rely on terrestrial or aquatic resources? (2) How do these proportions differ among the four species? (3) To what extent are differences in reliance on terrestrial versus aquatic resources a function of habitat selection or prey preferences?

2 | METHODS

2.1 | Study region

This study was conducted in lotic waterbodies in the Central Amazon region (Figure 1) and comprised three different hydrological sampling scales. The first scale covered first- to third-order pristine closed-canopy streams with headwaters that originate in the forests of the interfluve between the Purus and Madeira Rivers (Figure 1b). Stream order follows Strahler's modification of Horton's scale (Petts. 1994). In this region, streams are affected by local rainfall rather than the hydrological regimes of the main rivers and most of these streams dry out completely during some months (June-October, F. Villamarín, personal observation). Most headwater streams in the Amazon basin are nutrient poor (Furch, 1986; Furch & Junk, 1980), and their "black" waters are very poor in electrolytes, and low in pH and electrical conductivity. They support few submerged aquatic macrophytes and algal growth because of their low-light conditions (Junk et al., 2011) and are net heterotrophic as evidenced by low dissolved oxygen (see Table S1 in Supporting Information for detailed physicochemical information).

We sampled 250 m stretches from 55 pristine headwater streams clustered in 10 sampling modules. These clusters were distributed along an approximately 600 km transect throughout the interfluvial region of the Purus and Madeira Rivers (Figure 1b). This region is intersected by the Br-319 highway, a partially unpaved road that connects the cities of Manaus and Porto Velho and allows sampling of the otherwise inaccessible network of headwater streams. The sampling clusters are part of a research module network of the Research Program in Biodiversity (PPBio, http://ppbio.inpa.gov.br/sitios/br319).

The second hydrological sampling scale comprised third- to fifthorder flooded-forest streams and ria lakes within four sub-basins, which originate within the Purus–Madeira interfluve, and flow into the Purus River (Figure 1d). These wetlands are subject to predictable monomodal pulses of inundation (Jardine et al., 2015; Junk et al., 2011), with flood amplitudes that are greatest near the confluence with nutrient-rich "white" waters of large rivers and decline rapidly upstream (Junk et al., 2011). Ria lakes may be temporarily influenced by sediment-laden waters during high-water periods, but are filled by black waters when river levels are low (Junk et al., 2011).

The third hydrological sampling scale of this study covered the western margin of the Purus River, where large extensions of white water (sediment-laden) floodplains, locally known as várzeas extend for dozens of kilometres within the limits of the Piagacu-Purus Sustainable Development Reserve (PP-SDR) (Figure 1c). Várzea floodplains receive water, sediments and biological material from large parent rivers originating in the Andes and are subjected to long-lasting, monomodal and predictable flood pulses with high amplitudes (Junk et al., 2011). These are the most species-rich wetland forests in the world (Wittmann et al., 2006); they have mean flood periods of around 230 days/year (Junk et al., 2011) and have rates of net primary productivity of up to 33 Mg ha⁻¹ year⁻¹ (Megagram = 10⁶ g; Schöngart, Wittmann, & Worbes, 2010). Five waterbodies in várzea floodplains were sampled during crocodilian monitoring activities carried out by the Crocodilian Conservation Program of the Piagaçu Institute.

2.2 | Food-web sampling

Primary producers were collected at each study site to characterise isotope values at the base of the food web. Biofilm samples were obtained via toothbrush scrapes of submerged vegetation surfaces, such as leaves and twigs. Samples were placed in small ziplock bags with distilled water. In the field camp, the contents of the bags were transferred into capped cryogenic vials and stored in liquid nitrogen. Samples of stream water were collected and filtered in the field on glass-fibre filters (47 mm diameter, 0.6 μ m pore size). These filtered samples represent fine particulate organic matter (FPOM) in suspension as no phytoplankton growth was expected in these headwater streams. No submersed aquatic plants were found. Leaf-litter samples were collected from the stream margins, rinsed with distilled water and placed in ziplock bags. In most cases, these samples were collected from outside the water column, as many of the streams were dry when sampled.

Potential crocodilian prey groups, such as terrestrial and aquatic invertebrates, were captured according to their availability. Terrestrial invertebrates, such as coleopterans and ants, were captured by hand. Aquatic invertebrates and fish were captured using dipnets, in a 50 m stretch of each stream. Small fish (<50 mm standard length) were stored whole and a small piece of white dorsal muscle was collected from larger fish (>50 mm standard length). Claw samples from terrestrial vertebrates, such as agouti (*Dasyprocta* sp.) and paca (*Cuniculus* sp.), were obtained opportunistically from subsistence hunters in the area. While some samples of invertebrates and fish were preserved in ethanol for identification, all isotope samples collected from all trophic levels were kept frozen in liquid nitrogen for approximately 1 month before their return to the laboratory.

Crocodilians were captured using fyke nets in headwater streams and steel snares at night in other waterbodies. After measuring (SVL), sexing and weighing the animals, a piece of claw and a small WILEY Freshwater Biology



FIGURE 1 Study region. (a) Northern South America showing the Amazon Basin in grey. (b) Purus–Madeira interfluve region showing the three hydrological scales of this study surrounded by dashed lines. Numbers within the largest dash-lined region correspond to the 55 headwater streams studied. (c) Detail of the várzea floodplains region. (d) Detail of the region of mid-order flooded-forest streams and ria lakes. Symbols represent the four crocodilian species (*Paleosuchus trigonatus* = \circ , *P. palpebrosus* = \Box , *Caiman crocodilus* = \diamond , *Melanosuchus niger* = Δ). Gray scale colours in b, c and d represent water (black), non-flooded forests (dark grey) and floodplains (light grey)

piece of dorsal tail muscle underlying the scutes was removed and rinsed with distilled water to avoid contaminating the sample with blood. Claw tissue was used for isotopic mixing models as this was the tissue with the highest number of collected samples. However, in the case of *M. niger*, only one sample of claw tissue was available, the remaining were muscle–tissue samples. Thus, linear regressions were performed using muscle and claw tissues from the other three species to correct the values of muscle tissue in *M. niger* ($\delta^{13}C_{Claw} = -3.09 + 0.86 \times \delta^{13}C_{Muscle}$; $R^2 = .63$; p < .001; df = 61).

2.3 | SIA laboratory processing

All samples were kept frozen at -20° C in the laboratory. Biofilm samples were sieved using a 300- μ m mesh to remove larger detrital

material. The biofilm was then subsampled into a bulk fraction and a second sub-sample that was centrifuged using LUDOX[®]-TM50 colloidal silica following Hamilton, Sippel, and Bunn (2005).

All samples were dried in an oven at 60°C for 24–48 hr before grinding and homogenising with a mortar and pestle. Samples were combusted in a EuroEA 3000 (EuroVector, Italy) or Europa GSL (Sercon Ltd, Crewe, U.K.) elemental analyser and the resulting CO₂ and N₂ gases were chromatographically separated and fed into an Iso-Prime (Micromass, U.K.) or Hydra 20–22 (Sercon Ltd, Crewe, U.K.) isotope-ratio mass spectrometer. This measures the ratio of heavy and light isotopes in a sample relative to a standard. Isotope ratios (δ) are expressed in parts per mil (‰), defined as δ (‰) = ($R_{sample}/R_{standard} - 1$) × 1,000, where R_{sample} and $R_{standard}$ are the isotope ratios of the sample and standard respectively. Isotopic

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standards used were referenced to PeeDee Belemnite for carbon, and atmospheric air for nitrogen.

Although both $\delta^{13}C$ and $\delta^{15}N$ values were obtained for all samples included in this study, we used only $\delta^{13}C$ in the mixing model analyses due to uncertainty in $\delta^{15}N$ fractionation values and the limited differences in $\delta^{15}N$ values between our aquatic and terrestrial end-members.

2.4 Statistical analysis

We assessed differences in isotopic composition between primary sources using a one-way analysis of variance (ANOVA). Before performing ANOVA tests, we tested if our data met the assumptions of homogeneity of variances using Levene's test. When the assumptions were not met, we used Kruskal–Wallis non-parametric analysis of variance. Pairwise differences among primary sources were assessed using a Tukey's HSD post hoc test. Pairwise differences between centrifuged and bulk biofilm samples were assessed using a paired *t*-test. To estimate differences in δ^{13} C values of centrifuged biofilm samples as a function of habitat type, we used a Kruskal–Wallis test.

Differences in crocodilian isotopic composition as a function of taxon, habitat type, SVL and sex were assessed using an ANCOVA test with multiple factors in which the only continuous variable was SVL.

We performed a t-test to assess differences in $\delta^{13}C$ values between aquatic and terrestrial end-members sustaining each crocodilian species. A one-way ANOVA was performed to assess differences in aquatic and terrestrial end-member isotopic composition as a function of crocodilian species. Differences in $\delta^{13}C$ values of fish, which was the only aquatic prey group with available isotopic data from all the habitat types, were assessed using a Kruskal–Wallis test.

2.5 | End-member isotopic composition for mixing models

Isotopic mixing models using Bayesian frameworks (e.g. MixSIAR, SIAR) allow users to incorporate variation in source isotope values and trophic discrimination factors as well as prior information, such as stomach content data, thereby reducing uncertainty in mixing model predictions (Francis et al., 2011; Moore & Semmens, 2008; Parnell et al., 2013; Semmens, Ward, Moore, & Darimont, 2009; Stock & Semmens, 2013; Ward, Semmens, & Schindler, 2010). Unbalanced sample sizes of different prey organisms may lead to miscalculation of their relative contribution to end-member mean δ^{13} C values. For example, low-biomass prey that are easy to capture may be overrepresented in the sample, while larger, more energyrich prey that are only opportunistically sampled may be underrepresented. Therefore, isotope values of prey were aggregated into one of two major categories, either terrestrial or aquatic. We then used previous diet studies to calculate δ^{13} C weighted means and standard deviation using the proportion of recovered prey mass (Pérez, 1992; this study), per number of prey individuals per crocodilian size class (Magnusson et al., 1987) as weighting factors in the calculation. Crocodilians were grouped into six size classes: <20, 20.1–30, 30.1–40, 40.1–50, 50.1–60 and >60 cm SVL, and the weighted prey mean (g/crocodilian/size class) based on the number of individuals per size class in our sample, was calculated for each of the four species. All δ^{13} C values of these prey came from our sample set with the exception of those for *várzea* fish, which were obtained from Forsberg, Araujo-Lima, Martinelli, Victoria, and Bonassi (1993).

Calculations of end-member isotopic composition were assessed for each crocodilian species separately. Fish was the only aquatic group with available samples in all three habitat types and also the one with the most variation on biomass contribution to crocodilian diets. Therefore, *várzea* fish data were used to estimate isotopic composition of aquatic end-members for *M. niger*, a combination of *várzea* and headwater fish data were used for *C. crocodilus* and *P. palpebrosus*, and headwater fish data were used for *P. trigonatus*. Terrestrial end-member samples were available only from headwater habitats and we used these values for all crocodilian species. Endmember δ^{13} C mean and *SD* were used to run a one-isotope, twosource model in MixSIAR (Stock & Semmens, 2013).

2.6 | Model parameterisation

The MixSIAR mixing model parameterisation included three chains, a chain length of 100,000, burn-in interval of 50,000 and thin-by interval of 50. The trophic discrimination factor used was $1.2 \pm 0.1\%$ (Marques et al., 2014). Results are reported as medians with 95% Bayesian Credible Intervals (95% BCI) (Table 1).

2.7 | Model diagnostics

The Bayesian procedures within the MixSIAR framework include statistical diagnostic tests to assess MCMC convergence. The Gelman– Rubin test (Brooks & Gelman, 1998; Gelman & Rubin, 1992) is based on analysing multiple simulated MCMC chains by comparing the variance within each chain to the variance between chains. Large deviation between these variances indicates non-convergence and the ratio will be near 1 at convergence. The Geweke test (Geweke, 1991) is a two-sided *z*-test comparing the mean of the first part of the chain with the mean of the second part. At convergence, these

TABLE 1 Median estimates of aquatic and terrestrial proportional contributions in Amazonian crocodilian diets derived from MixSIAR mixing models. 95% Bayesian Credible Intervals (BCI) are shown in parentheses

	Median (95% BCI)	
Species	% Terrestrial	% Aquatic
Paleosuchus trigonatus	58 (47–68)	42 (33–54)
P. palpebrosus	30 (17–41)	70 (59–83)
Caiman crocodilus	34 (14–48)	66 (52–86)
Melanosuchus niger	21 (2–35)	79 (65–98)

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means should be the same, and large absolute *z*-scores indicate that the result should be rejected.

2.8 | Diet overlap

To compare the posterior estimates of source contributions among crocodilian diets, pairwise Bhattacharyya coefficients (BC; Bhattacharyya, 1943), defined as an approximate measurement of the amount of overlap between two statistical samples, were calculated. This coefficient will be 0 if there is no overlap and can reach 1 when the samples are completely overlapping (Bond & Diamond, 2011).

2.9 | Spatial analysis

To further assess occupation of the different aquatic habitat types (headwaters, flooded-forest streams and várzea floodplains; see Study region) and how habitat use influenced diet, the extent of non-flooded forest surrounding each sampled individual was assessed. A larger proportional area of non-flooded forests around individuals indicated that aquatic habitats became smaller towards the headwaters. A classified image map of wetland extent, vegetation type and dual-season flooding state of the entire lowland Amazon basin was used (Hess et al., 2015). The classified image was derived from the Global Rain Forest Mapping Project Amazon mosaics (Rosenqvist et al., 2002; Siqueira et al., 1999) acquired during October-November 1995 and May-June 1996 (see Hess et al., 2015 for details of classification procedures). From this map, spatial analysis R packages sp and raster (Hiimans & Van Etten, 2014; Pebesma & Bivand, 2005) were used to calculate the proportion of non-flooded forest present in a 1 km radius around each of the captured crocodilians. Multiple regression models were then used to estimate the influence of the proportion of non-flooded forest and crocodilian body length (SVL) on δ^{13} C values. Finally, assuming that adult Amazonian crocodilians, especially Paleosuchus spp., have small home ranges (Magnusson & Lima, 1991), pairs of individuals of different species captured within a maximum distance of 200 m of each other were compared using paired t-tests on $\delta^{13}C$ values to determine if they had similar prey bases. All statistical analyses and graphics were run using R software (R Development Core Team, 2016).

3 | RESULTS

At the first hydrological scale, a total of 55 first- to third-order headwater streams were sampled. Within these headwater sites, 30 *P. trigonatus*, 8 *P. palpebrosus* and 6 *C. crocodilus* individuals were captured. Further downstream, in the second hydrological scale, four sub-basins comprising third- to fifth-order flooded-forest streams and ria lakes that flow into the Purus River were sampled, and 15 *P. trigonatus* individuals, 28 *P. palpebrosus* individuals and 6 *C. crocodilus* individuals were captured. On the opposite margin of the river, in *várzea* floodplains, one *P. palpebrosus* individual, four *C. crocodilus* individuals and nine *M. niger* individuals were captured. Mean \pm *SD* δ^{13} C values measured in crocodilians were highest in *P. trigonatus* (-25.7 \pm 1.2‰), intermediate in *C. crocodilus* and *P. palpebrosus* (-27.4 \pm 1.5‰; -27.7 \pm 1.1‰ respectively) and lowest in *M. niger* (-29.9 \pm 1.3‰; Figure 2). Although not used in mixing models and other analyses, mean δ^{15} N values in crocodilians varied from 7.1‰ to 8.2‰, while prey items ranged from 2.5‰ in Formicidae to 10.1‰ in Erythrinid fish. The range of variation in SVL was 23.8–99.2 cm in *P. trigonatus*, 17.4–96.4 cm in *P. palpebrosus*, 30.3–97.8 cm in *C. crocodilus* and 56.5–105.5 cm in *M. niger*.

Mean \pm SD δ^{13} C values measured in primary producers were lowest in C3 leaf litter (-33.1 \pm 1.6‰), intermediate in bulk biofilm (-31.5 \pm 1.4‰) and highest in suspended FPOM (-29.5 \pm 0.8‰). These three sources were statistically different (ANOVA: $F_{2,75} = 13.52$; p < .001), but their distributions overlapped considerably. Pairwise differences among all sources were significant according to a Tukey's HSD post hoc test (p < .027 in all cases). Bulk biofilm samples showed no statistical differences from centrifuged samples (-31.5 \pm 2.7‰) (Student's *t*-test: t = -0.11, df = 78.8, p = .915). Furthermore, no statistical differences were found in centrifuged biofilm samples collected in headwater, mid-order floodedforest streams and *várzea* floodplains (Kruskal–Wallis $\chi^2 = 3.3$, df = 2, p = .19).

We found a significant effect of taxon (ANOVA $F_{3,98} = 43.4$; p < .001) and habitat type ($F_{2.98} = 10.8$; p < .001), but not of SVL $(F_{1,98} = 1.3; p = .262)$, nor sex $(F_{2,98} = 1.3; p = .280)$, on δ^{13} C values of all species together. However, when we analysed each species separately, multiple regression models ($\delta^{13}C = -29.8 + 0.02_{SVL} +$ 3.18_{NFF} ; $F_{2.42} = 12.5$, $R^2 = .37$, p < .001) indicated that variation in P. trigonatus δ^{13} C values was predicted by both body length (SVL; p < .001) and the proportion of non-flooded forest (NFF; p < .001). This relationship was different for P. palpebrosus ($\delta^{13}C =$ $-30.01 + 0.008_{SVL} + 2.75_{NFF}; F_{2.31} = 13.57; R^2 = .47; p < .001),$ where the proportion of non-flooded forest had a significant effect (p < .001) on δ^{13} C values, but body length did not (p = .204). In contrast, δ^{13} C values in C. crocodilus (δ^{13} C = -24.3 - 0.06_{SVI} + 0.84_{NFF}; $F_{2,28} = 8.4$; $R^2 = .38$; p = .001) varied as a function of body length (p = .011), but not the proportion of non-flooded forest (p = .434). In M. niger, the multiple regression including both body length and the proportion of non-flooded forest was not statistically significant $(F_{1,7} = 0.49, R^2 = .06, p = .505)$, but the low sample size precludes confidence in this result.

Aquatic and terrestrial prey end-members sustaining all four crocodilian species were significantly different in δ^{13} C values (t-test: t > 14; df > 108; p < .001 in all cases, see Tables S2 and S3). Despite leaf litter having lower δ^{13} C than biofilm, terrestrial prey were enriched in ¹³C relative to aquatic prey.

Fish and terrestrial vertebrates represented the bulk of prey mass found in previous stomach content studies and end-member values were more similar to the isotopic composition of these prey (Table S1). Terrestrial end-member δ^{13} C values did not differ among species (ANOVA: $F_{3,396} = 0.2$; p = .89), whereas aquatic end-members composing *M. niger* diet were more depleted in ¹³C than those of the other three crocodilians ($F_{3,396} = 29.2$; p < .001, Table S1).



FIGURE 2 Isospace of crocodilians and end-members. Graphic representation of isotopic composition of the four caiman species (a-d). aquatic (e) and terrestrial (f) end-members. The size of end-member symbols is proportional to their relative biomass contribution to crocodilian diets

Fish was the only group of aquatic prey for which $\delta^{13}C$ data were available from all three habitat types. The δ^{13} C values of fish from headwater, mid-order streams and várzea floodplains were significantly different according to a Kruskal–Wallis test ($\chi^2 = 21.16$, df = 2, p < .001).

MixSIAR models converged satisfactorily. Out of 13 variables, the Gelman-Rubin diagnostic yielded only one value >1.05. For the Geweke diagnostic, only two variables were outside ± 1.96 in one chain. For all individuals, independent of species, terrestrial resources made a predicted median proportional contribution of 36%, against 64% from aquatic inputs. However, these proportional contributions differed among species. P. trigonatus had the highest estimated median proportional contribution from terrestrial resources (58%), as opposed to the other species in which terrestrial inputs progressively decreased. C. crocodilus, P. palpebrosus and M. niger had 34%, 30% and 21% respectively (Figure 3 and Table 1). Overall, BC were near 0.5 for all species pairs (Table 2), suggesting c. 50% overlap of diet. Of all species pairs, C. crocodilus and P. palpebrosus showed the highest diet overlap (BC = 0.55) and P. trigonatus and M. niger had the lowest overlap (BC = 0.51) (Table 2).

Individuals of P. trigonatus were captured together with P. palpebrosus at 15 locations and with individuals of C. crocodilus at four locations, but not with individuals of M. niger. Paleosuchus palpebrosus individuals were captured sharing space with C. crocodilus in nine locations but only in one location with M. niger. Caiman crocodilus and M. niger were captured together in seven locations. Values of δ^{13} C of syntopic individuals of different species were significantly different for the congeners P. trigonatus and P. palpebrosus (paired t-test: t = 4.12, df = 14, p = .001, Figure 4), but not for other species pairs: P. trigonatus and C. crocodilus (t = -1.19, df = 3, p = .319); P. palpebrosus and C. crocodilus (t = -1.31, df = 8, p = .228); C. crocodilus and M. niger (t = -0.86, df = 6, p = .422).

DISCUSSION 4

Combining stable isotope and spatial analyses, we found evidence of differences in resources supporting Amazonian crocodilians in an ecotone comprising headwater streams, mid-order flooded-forest streams and várzea floodplains. Mean δ^{13} C values were highest in



TABLE 2 Pairwise comparisons of median Bhattacharyya coefficients estimating overlap in dietary source proportions in four Amazonian crocodilian species. Lower (LCL) and upper (UCL) 50% confidence limits are given in parentheses

	Melanosuchus niger Median (LCL-UCL)	Paleosuchus palpebrosus Median (LCL-UCL)	P. trigonatus Median (LCL-UCL)
Caiman crocodilus	0.54 (0.31–0.78)	0.55 (0.37–0.74)	0.54 (0.5–0.59)
M. niger		0.54 (0.29–0.80)	0.51 (0.39–0.63)
P. palpebrosus			0.54 (0.47–0.60)

P. trigonatus from headwaters, intermediate in *C. crocodilus* and *P. palpebrosus* in flooded-forest streams and lowest in *M. niger* in *várzea* floodplains. The progressive decrease in δ^{13} C values of crocodilians occurred from headwaters to floodplains. This reflects an increasing downstream reliance on aquatic over terrestrial resources and mirrors the way these sympatric predators are distributed along this ecotone. However, when taking into account the influence of habitat type by analysing pairs of syntopic individuals of different species, significant differences in δ^{13} C values suggest that *P. trigonatus* and *P. palpebrosus* have different prey bases when in syntopy, so species differences probably result from prey preferences in addition to habitat selection.

Most crocodilians are considered generalist, opportunistic predators (Pooley, 1989) that take advantage of any available source of

FIGURE 3 Posterior distributions produced by the MixSIAR simulations. Terrestrial and aquatic resources are represented in dark and light grey, respectively, for *Paleosuchus trigonatus* (a), *P. palpebrosus* (b), *Caiman crocodilus* (c), and *Melanosuchus niger* (d)



FIGURE 4 Interspecific isotopic comparisons. Pairwise comparisons of δ^{13} C values between individuals of *Paleosuchus trigonatus* (•) and *P. palpebrosus* (□) in 15 sites where they were captured syntopically

ingestible animal protein of adequate size. Amazonian crocodilians partition space, each species occurring most frequently in specific habitats (Magnusson, 1985), so it is expected that their diets will vary depending on the availability of different prey in each habitat type (Magnusson et al., 1987).

Paleosuchus trigonatus and the African dwarf crocodile, Osteolaemus tetraspis, are the only extant crocodilians known to thrive in headwater streams under closed-canopy forests (Magnusson, 1985). In the streams we studied, terrestrial resources represented almost

60% of carbon inputs contributing to P. trigonatus tissues. This is expected for a species that lives in headwater streams where large terrestrial prey are readily available. These prey may provide greater sources of organic matter in terms of biomass than crustaceans and small fish (which commonly grow to less than 25 mm standard length). The primary carbon sources sustaining the terrestrial vertebrates are most likely derived from forest trees (C3 sources). Vertebrates comprised more than 99% of the biomass of terrestrial end-members in the diet of P. trigonatus in this study. Most carbon inputs probably originate from tree fruits and seeds, as they represent the main food sources for forest-floor herbivores, such as species of Dasyprocta and Cuniculus (Dubost & Henry, 2006). Nonphotosynthetic parts of trees, such as reproductive and woody stem parts, usually show higher δ^{13} C values than leaves (Blumenthal, Rothman, Chritz, & Cerling, 2015; Martinelli et al., 1998; Medina & Minchin, 1980). Furthermore, ¹³C-depleted samples of leaf litter may be caused by uptake of respired CO₂ in the forest understory (Medina & Minchin, 1980). These factors may explain why our C3 leaf-litter $\delta^{13}C$ values were around 8% lower than those of terrestrial prey. Fruits and flowers had mean $\delta^{13}C$ values of $-26.5\pm1.6_{\rm oo}^{\prime}$ in a closed-canopy tropical African forest (Blumenthal et al., 2015). Although we do not have estimates of fruit δ^{13} C values from our study area, the values reported by Blumenthal et al. (2015) match well with those of keratin tissue from Cuniculus and Dasvprocta in our study.

Headwater streams receive significant carbon inputs from litter fall from C3 trees, with litter fall rates of >10 Mg ha^{-1} year⁻¹ occurring in lowland tropical regions (Naiman, Decamps, & McClain, 2010). Allochthonous resources, whether from trees or other sources, enter streams as coarse particulate organic matter that degrades to FPOM and accumulates on underwater surfaces. When deposited, FPOM particles mix with live algae, algal detritus and detritus of terrestrial or aquatic vascular plant origin (Hamilton et al., 2005). This conglomerate of allochthonous and autochthonous matter, known as biofilm, is common in streams and could represent a second pathway by which terrestrial carbon reaches crocodilians via consumption of small fish that feed on biofilm and detritus. However, as the potential contribution of end-members was weighted by the estimated volume consumed, and the large várzea fish would not eat biofilm from streams, this had little effect on estimates of primary sources contributing to crocodilian diets.

Although low in biomass, periphyton within the biofilm most likely represents the only source of autochthonous inputs in the shaded environments of forest streams, as no phytoplankton growth is expected. In these conditions, contributions of microalgae and allochthonous resources are often difficult to distinguish using stable isotopes as both resources often overlap in δ^{13} C values in headwater streams (Finlay, 2004; France, 1995; Jardine, Kidd, & Cunjak, 2009). This occurs as the result of isotopic overlap and the contamination of the autochthonous samples with allochthonous detritus (Jardine et al., 2009). The first problem is difficult to deal with, but the latter can potentially be overcome by centrifuging biofilm samples with colloidal silica and physically separating micro-algae from detritus (see Hamilton et al., 2005). In this study, even after centrifuging biofilm in colloidal silica, we found no significant differences in δ^{13} C values between bulk and centrifuged samples, with few exceptions. Since bulk biofilm samples consist mostly of allochthonous FPOM, little micro-algae was present in our samples, a reflection of what is expected in unproductive closed-canopy streams (Fisher & Likens, 1973).

When there is relatively poor distinction of isotopic compositions between sources, other information can be used to parameterise MixSIAR models (Moore & Semmens, 2008; Soto, Benito, Gacia, García-Berthou, & Catalan, 2016). We were able to estimate the relative importance of carbon inputs from aquatic versus terrestrial resources in the isotopic composition of caiman tissues by using prior information of the relative mass contributions of prey to define end-member δ^{13} C means and SD. Caiman crocodilus and P. palpebrosus are often found occupying mid-order stream channels and flooded-forest habitats in syntopy. Some P. trigonatus may also be found sharing the same habitats. More autochthonous primary production is expected in the lower reaches than in the headwaters as stream channels widen progressively and the quantity of light reaching streams increases (Naiman, Melillo, Lock, Ford, & Reice, 1987). Although not quantified in this study, if this is the case in these streams, the increasing amounts of autochthonous carbon entering the food web are expected to be progressively incorporated in higher trophic levels, such as fish and crocodilians. Furthermore, fish size increases downstream as the waters become deeper (Harvey & Stewart, 1991; Schlosser, 1982). Crocodilian species living in the mid-reaches of these streams apparently benefit more from such prey than from terrestrial vertebrates. Consequently, isotopic inputs from aquatic resources are greater for both P. palpebrosus and C. crocodilus than for P. trigonatus. On the other hand, low algal production in headwater streams may cause aquatic consumers, such as invertebrates and fish, to rely mainly on terrestrial carbon. This means that even the small percentage of aquatic prey found in the diet of headwater crocodilians is probably sustained by terrestrial carbon (but see Brito, Moulton, De Souza, & Bunn, 2006; Lau, Leung, & Dudgeon, 2009; Neres-Lima et al., 2016).

Further downstream, várzea floodplains are extremely productive habitats (Junk, Bayley, & Sparks, 1989; Schöngart et al., 2010), and it is there that M. niger reaches its highest densities (Da Silveira, 2002). In these floodplains, M. niger and C. crocodilus occur syntopically, sharing foraging areas (Marioni, Da Silveira, Magnusson, & Thorbjarnarson, 2008) and partitioning nesting sites (Villamarín et al., 2011). Considerable amounts of fish in the diet of adult M. niger are responsible for their high reliance on aquatic resources. Floodplain fish included in this study are ¹³C-depleted (δ^{13} C mean \pm SD = -33.9 \pm 1.2%), as they are supported by carbon from phytoplankton (Forsberg et al., 1993). Phytoplankton mean δ¹³C values in central Amazon várzea floodplains are low, varying between -40% and -30% (Araujo-Lima, Forsberg, Victoria, & Martinelli, 1986; Caraballo, Forsberg, & Leite, 2014; Forsberg et al., 1993; Mortillaro et al., 2015).

Significant differences in δ^{13} C values of caiman tissues suggest different proportions of terrestrial or aquatic resources sustaining these species. However, differences in diets may be a reflection of WILEY Freshwater Biology

spatial distributions of these sympatric species (Magnusson et al., 1987; this study). BC derived from posterior distributions of Mix-SIAR models showed overall overlaps in carbon inputs of around 50% among pairs of Amazonian crocodilian species. However, since the mixing models did not explicitly take into account spatial distributions, this is not by itself strong evidence of syntopic resource partitioning.

When taking into account habitat by selecting pairs of individuals of different species occurring syntopically, we found significant differences in δ^{13} C between P. trigonatus and P. palpebrosus. This suggests partitioning of prey resources between these closely related species that is not caused simply by habitat selection. Evidently, even in locations where aquatic prey are more readily available, P. trigonatus exploits more terrestrial prey than P. palpebrosus. This might be facilitated by its terrestrial habits, as it is commonly found inside terrestrial retreats up to 90 m from streams (Magnusson & Lima, 1991). Morphological adaptations may be related to higher efficiency in consuming certain groups of prey. Analysis of skull shape shows divergences between the two species of Paleosuchus within morphometric space. In fact, P. palpebrosus is closer to M. niger and C. crocodilus than to its congener, P. trigonatus, within skull morphospace (Pierce, Angielczyk, & Rayfield, 2008). This observation is in agreement with our findings on interspecific isotopic patterns which mirror the spatial distribution of Amazonian crocodilians. However, the interpretations of Pierce et al. (2008), suggesting higher ingestion of fish and terrestrial prey by long and broadsnouted crocodilians, respectively, are not supported by our data set. In fact, Amazonian crocodilians show the opposite pattern: P. trigonatus with a long narrow skull seems to be more adapted for preying on medium-sized terrestrial animals, while P. palpebrosus with a broader skull is evidently ingesting more fish, as do the other two species. Magnusson (2015) suggested that skull shape is more related to the difficulties caused by dense vegetation than by the type of prey. These contrasting sources of evidence suggest that the relationship between morphological adaptations and food habits is complex and further studies that include morphological and dietary analysis, taking into account habitat characteristics, are needed in order to make broad generalisations.

In this study, we found interspecific differences in the proportions of terrestrial and aquatic carbon inputs sustaining Amazon crocodilians. This advances understanding of the ways that energy flows between aquatic and terrestrial food webs in these habitats. Our results suggest that despite being considered opportunistic generalist predators, Amazon crocodilians have diet divergences resulting not only from habitat selection but also from prey preferences. Thus, these species show some degree of specialisation that may contribute to avoiding competitive exclusion in these waterbodies. Furthermore, reliance on different carbon resources varies in some species also as a function of body length (e.g. Davis, Blanchette, Pusey, Jardine, & Pearson, 2012; this study). Thus, ontogenetic shifts in reliance on aquatic or terrestrial carbon resources might be related to the way that individuals of different sizes are distributed in space. Since differences in body length can limit competition, intraspecific differences in isotopic composition of crocodilians might be as important as interspecific differences, a subject that deserves further investigation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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